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Abstract Visual information processing is adapted to the statistics of natural visual stimuli, and these statistics depend to a large extent on the movements of an animal itself. To investigate such movements in freely walking blowflies, we measured the orientation and position of their head and thorax, with high spatial and temporal accuracy. Experiments were performed on *Calliphora vicina*, *Lucilia cuprina* and *L. caesar*. We found that thorax and head orientation of walking flies is typically different from the direction of walking, with differences of 45° common. During walking, the head and the thorax turn abruptly, with a frequency of 5–10 Hz and angular velocities in the order of 1,000°/s. These saccades are stereotyped: head and thorax start simultaneously, with the head turning faster, and finishing its turn before the thorax. The changes in position during walking are saccade-like as well, occurring synchronously, but on average slightly after the orientation saccades. Between orientation saccades the angular velocities are low and the head is held more stable than the thorax. We argue that the strategy of turning by saccades improves the performance of the visual system of blowflies.

Keywords *Calliphora vicina* · *Lucilia* · Optic flow · Saccade · Search coil

Introduction

Visual systems are believed to be adapted to the processing of naturally occurring visual input (e.g., Atick 1992; van Hateren 1992; review: Simoncelli and Olshausen 2001). An animal must move in its environment, and the movements of its body, head and eyes cause changes in the image projected onto the retina. The vector field of local movements of the visual stimulus, due to eye movements or moving objects in the environment, is named the "optic flow" field. The optic flow due to eye movements has a rotational and a translational component, caused by rotations and translations of the eye, respectively (Koenderink 1986). The translational component of the optic flow can be used for the extraction of the 3D structure of the environment, whereas the rotational component gives no information on this structure (Koenderink and van Doorn 1987). Although it is possible to disentangle the rotational and translational components of a complex optic flow (Nagle et al. 1997), most animals already minimize the rotational optic flow before the first stage of vision, by performing short and fast saccadic eye movements between periods of fixation, i.e., steady gaze (Land 1999). During fixation, the rotational component is kept to a minimum, and during the saccade, the angular velocity is high only for a short time. Therefore, apart from the easier processing of translational flow, a further advantage of the strategy of saccadic eye movements is that the time of blurred vision is minimized. Saccadic eye movements must cause an important improvement of vision, because they are used by most animals from different phyla, from insects to primates (goldfish: Easter et al. 1974; crab: Paul et al. 1990; blowfly: Land 1973; Schilstra and van Hateren 1998b; man: e.g., Carpenter 1988). For a review, see Land (1999).

Since the natural visual input is to a large extent determined by the movements of the animal itself, it is important to study these movements during normal behaviour. Most existing methods of recording natural insect movements are based on video techniques (Sandström et al. 1996; Fry et al. 2000; Kern et al. 2001; Tammero and Dickinson 2002). These techniques have at least one of the following limitations: limited temporal resolution (commonly 50 Hz), limited spatial resolution, not allowing the reconstruction of all three

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coordinates of the orientation of the thorax, not resolving the orientation of the head of a freely walking or flying insect. Although they give an indication about the natural movements of the animal, the fine structure of the movements, and especially the fine structure of head movements, cannot be detected. Recent advances like pan-tilt cameras (Fry et al. 2000) and the use of two cameras (Tammero and Dickinson 2002) improved the performance significantly, but still do not allow a complete reconstruction of the head movements of a freely moving insect.

Apart from the video techniques, there is one method employing search coils (Schilstra and van Hateren 1998a), which has been previously applied to the study of flying insects. It allows the simultaneous reconstruction of the head and thorax orientation with high spatial and temporal resolution, permitting a complete reconstruction of the spatio-temporal visual input. A disadvantage of the technique compared with video recording is the attachment of coils and wires to the fly. For the measurements presented here this is not a problem (see Materials and methods). We use the method to study the normal walking behaviour in several species of blowflies. Before the present study the movements of the eyes of freely walking flies had not been measured, and thus it was not known whether the eyes perform saccades during walking. We therefore extended the measurements on flying *Calliphora* to walking *Calliphora*, and to flying and walking *Lucilia*.

Materials and methods

Flies and coils

Experiments were performed on female blowflies; walking results are based on three specimens of *Calliphora vicina*, two of *Lucilia cuprina* and two of *L. caesar*. The position and orientation of the head and thorax of the flies walking in a cage was recorded by attaching small coil triplets to the flies. These coil triplets pick up externally applied magnetic fields and from these signals position and orientation can be reconstructed (Schilstra and van Hateren 1998b).

Attaching coils to the head and thorax may potentially interfere with normal movements. Therefore, we took into account the control experiments of van Hateren and Schilstra (1999) for determining the maximum acceptable coil sizes. They found that, for *C. vicina*, coils of 40 windings (2 mm diameter, triplet weight 0.8 mg) attached to the head, and 80 windings (2 mm, 1.6 mg) attached to the thorax, had a negligible effect on the head and thorax motion during flying. We used coils of the same dimensions in the present study on walking *Calliphora*. Because accelerations, both of translation and of rotation, are considerably lower during walking than during flying, we expect that the effect of the coils is also negligible in this case. *Lucilia cuprina* is smaller than *C. vicina*, and the body mass of the former (approximately 45 mg for the flies used in this study) is almost three times lower than the body mass of the latter (approximately 130 mg for the flies used in this study). The head weight is approximately the same for both species. An additional problem with *Lucilia* is that the small size of the fly does not allow coils of 2 mm to be attached to both head and thorax: they would touch each other. We therefore used coils of 1 mm diameter (40 windings, triplet weight 0.2 mg) for the head of *Lucilia*, and coils of 2 mm diameter (40 windings, 0.8 mg) for the thorax. We expect that the effect of these coils (proportionally smaller than those used for *Calliphora*) on normal movements is negligible.

Preparation, experiment and data processing

Preparations for attaching the coils were similar to those used by van Hateren and Schilstra (1999). The main difference is that, for walking experiments, we clipped the tips of the flies' wings. The clipped wings were not beating in the experiments presented here. The walking arena consisted of a cylinder of 225 mm diameter and 80 mm height, with the side wall covered by a pattern of smoothed black and white squares (50% probability of occurrence), each subtending 10° when viewed from the centre of the cage. The bottom was covered with a texture of light grey squares on a dark grey background (side length 5 mm, 0.5 squares cm^{-2}). The ceiling was transparent, giving a clear view of the opaque ceiling, 18 cm above, of the surrounding cage (opaque white with dark grey squares). Mean luminance was 150 cd m^{-2} at the walls and 800 cd m^{-2} at the ceiling. The flies were fed with water and sugar, and then released in the arena. Every 2–3 h the flies were fed again, and the cables were checked for loops, which would have hindered free walking.

The technique for measuring the position and orientation of the head and thorax is described by Schilstra and van Hateren (1998a). The accuracy of the method with the coils used for *Calliphora* is approximately 1 mm, 0.3°, and 1 ms. The coils used for *Lucilia* had fewer windings and a smaller diameter for the head triplet, and thus picked up less magnetic flux. The decreased signal strength and decreased signal-to-noise ratio reduced the accuracy to an estimated 2 mm and 0.5°. We will therefore concentrate in this article on the results obtained on *Calliphora*, and only discuss the results for *Lucilia* where appropriate.

The reconstructed data were low-pass filtered with a two-sided exponential filter, with time constants of 15 ms for position, 5 ms for head orientation, and 3 ms for thorax orientation. Walking and turning velocities were computed by differentiating position and yaw angle, respectively. For the analysis, we only used data that corresponded to walking (see Results for a definition of walking and breaks).

Slight variations in the alignment of the coil triplets from fly to fly were corrected by centring the distribu-

tions of head and thorax roll and pitch, adjusting the thorax yaw angle such that a symmetrical distribution of transverse horizontal velocity of the thorax resulted, and centring the distribution of the head yaw angle in the thorax coordinate system. All necessary corrections were smaller than 10°.

Angular coordinates

The spatial orientation of an object is described by three angles corresponding to an ordered sequence of rotations about three orthogonal axes, and starting from a reference orientation. We use here the Fick convention, which is a passive reference system—meaning that the reference system, including the object, rotates about its own axes in a fixed sequence (Haslwanter 1995): a rotation about the vertical axis of the object, followed by a rotation about its transverse axis, and then by a rotation about its longitudinal axis. Each rotation is thus performed about an axis resulting from the previous rotation. In the present article, unless stated otherwise, orientational angles refer to yaw, i.e., rotation about the vertical axis. The yaw velocity is calculated in the coordinate system attached to either the thorax or the head, instead of the laboratory coordinate system.

Results

Figure 1 presents 1 s of walking of a *C. vicina*. The curved line shows the trace described by the thorax and the short line segments show the yaw orientation of the head (gray) and thorax (black), with a time interval between successive segments of 10 ms. The intersection between the line segments and the trace indicates the position of the thorax. The fly starts walking from the top right of the figure, and proceeds via the bottom left to the top left.

The most striking feature of walking observed from this graph is that the orientation of the thorax is often misaligned with the direction of walking, thus the fly walks sideways for large parts of the trajectory. For example, at the beginning of the walking trace (top right), the difference is almost 90°. Careful examination of the figure reveals that there are even short sections where the fly is walking backwards, just after the sharp ($>90°$) turn (bottom). The direction of walking may change abruptly, but the orientation of the thorax generally changes during 1–2 cm of walking. Changes in the walking trajectory are largely independent of changes in body and head orientation because abrupt changes in the walking trajectory do not necessarily coincide with similarly abrupt changes in body and head orientation (e.g., Fig. 1, bottom left). On average, however, the body orientation tends to align with the walking trajectory. As a consequence of the differences between changes in walking trajectory and orientation, the thorax orientation is often significantly different from the direction of walking. We found this difference between the orientation and direction of walking in all flies from the three species we investigated (*C. vicina*, *L. cuprina* and *L. caesar*).

Another interesting feature that can be seen in Fig. 1 is that the head is roughly aligned with the thorax, typically within 5°. Thus the fly does not orient its head towards the direction of walking in order to offset the thorax misalignment, although it is capable of turning the head by up to 20° (Hengstenberg et al. 1986).

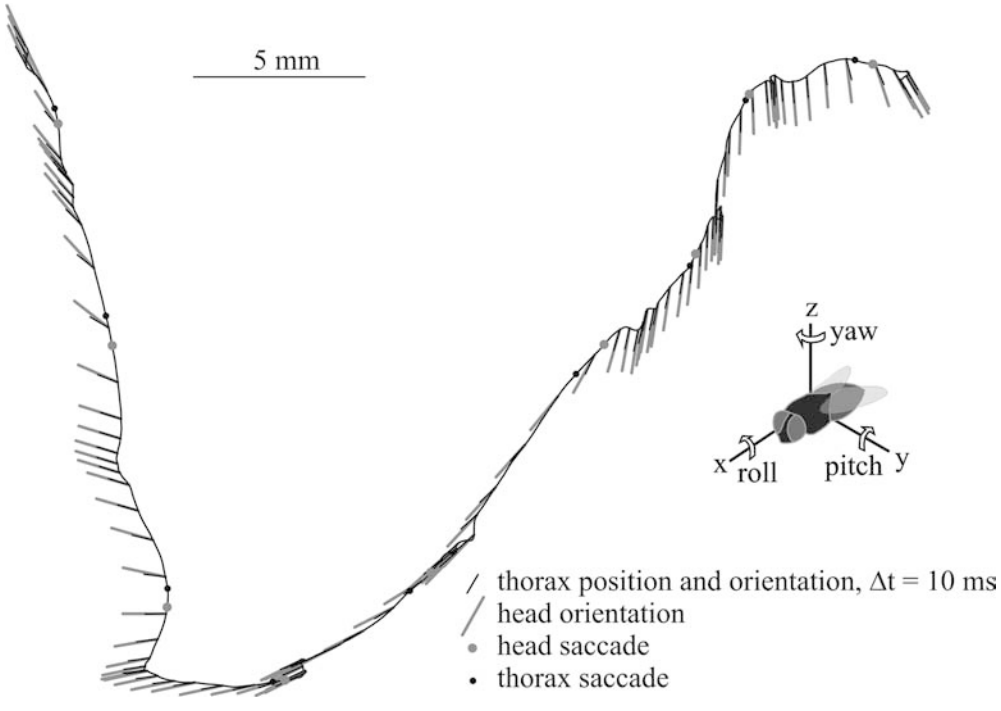

Fig. 1 Walking path of a blowfly during 1 s. The *curved line* shows the trajectory described by the thorax centre. *Line segments* indicate position and orientation of the head (*grey*) and thorax (*black*) every 10 ms. *Large dots* indicate positions of head saccades (peak velocities) and *small dots* indicate thorax saccades (peak velocities)

In order to investigate the relationship between thorax orientation and the direction of walking, we have plotted the yaw angle (Fig. 2a) and x and y coordinates of the thorax (Fig. 2b) during 3 s of walking (other segment than in Fig. 1). It is apparent from the graphs that yaw angle and position coordinates are composed of intervals of almost constant orientation or position, interrupted by fast saccadic turns or position changes. We will designate as "orientation saccades" the fast saccadic turns and as "position saccades" the fast position changes.

Figure 2c depicts the yaw velocity (corresponding to Fig. 2a), and gives an indication of the frequency and angular velocity of thorax orientation saccades. They are brief (in the order of 30 ms), with an angular velocity in the order of 1,000° s^{-1}, and follow each other at a rate of 5–10 Hz. Between saccades, the thorax orientation is almost constant. The thick line in Fig. 2d shows the total walking velocity (length of the velocity vector). Peak walking velocities correspond to position saccades. Unlike the intervals between orientation saccades where the yaw angular velocity returns to zero, in between position saccades there are troughs of lower walking velocity. These troughs do not become zero, indicating that the fly does not stop walking. Only during complete breaks both angular velocity and walking velocity become zero (e.g., at 2.5 s in Fig. 2). The thin line in Fig. 2d, superimposed on the walking velocity, represents the absolute yaw velocity (from Fig. 2c), and is shown (without vertical scale) on the same graph with the walking velocity to facilitate the comparison of the timing of position and orientation saccades. It is apparent that almost every peak in the walking velocity corresponds to a peak of the absolute yaw velocity, thus the saccades of thorax orientation and position occur at roughly the same time. However, there seems to be no correlation between the sizes of the corresponding saccades. On average, the peak walking velocity is attained 9.3 ± 17.7 ms (mean $\pm$ SD) after the peak yaw velocity. Thus there is a slight ordering of the orientation and position saccades, which can also be observed in Fig. 2d.

Figure 3 depicts the yaw, pitch and roll of the head and thorax for the short walk shown in Fig. 1. Thick

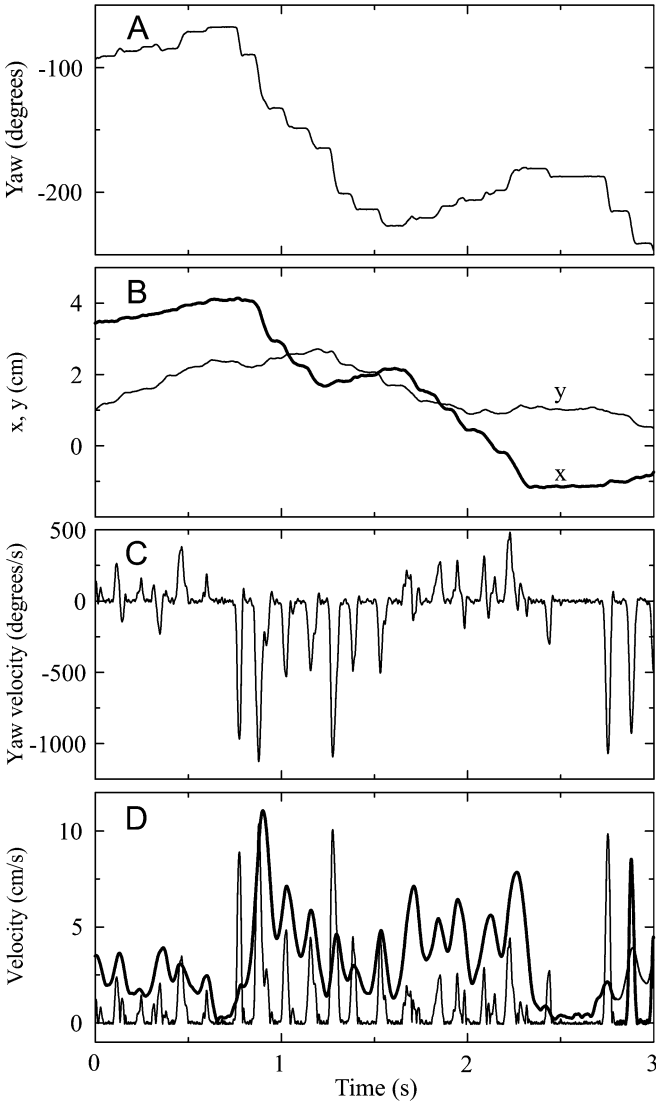

Fig. 2a–d Orientation, position, and velocities during 3 s of walking (other segment than in Fig. 1). **a** Yaw angle of the thorax. **b** x and y position of the thorax. Note that orientation and position change stepwise (through saccades). **c** Yaw velocity. **d** Walking velocity (*thick line*) and absolute yaw velocity (*thin line*; vertical scale not shown, trace is the absolute value of Fig. 2c). Peaks of the walking velocity have corresponding peaks in the yaw velocity

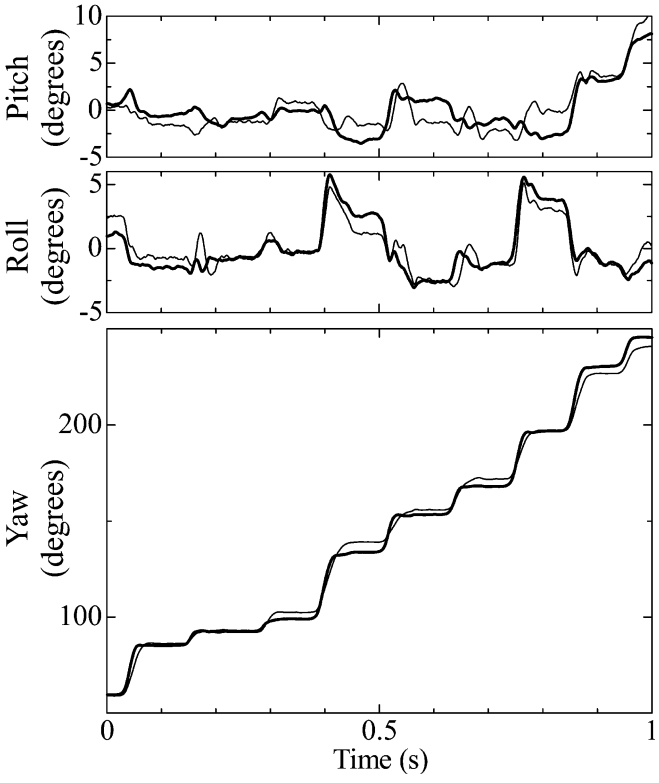

Fig. 3 Yaw, pitch and roll of head and thorax during 1 s of walking. Note the saccadic changes in yaw

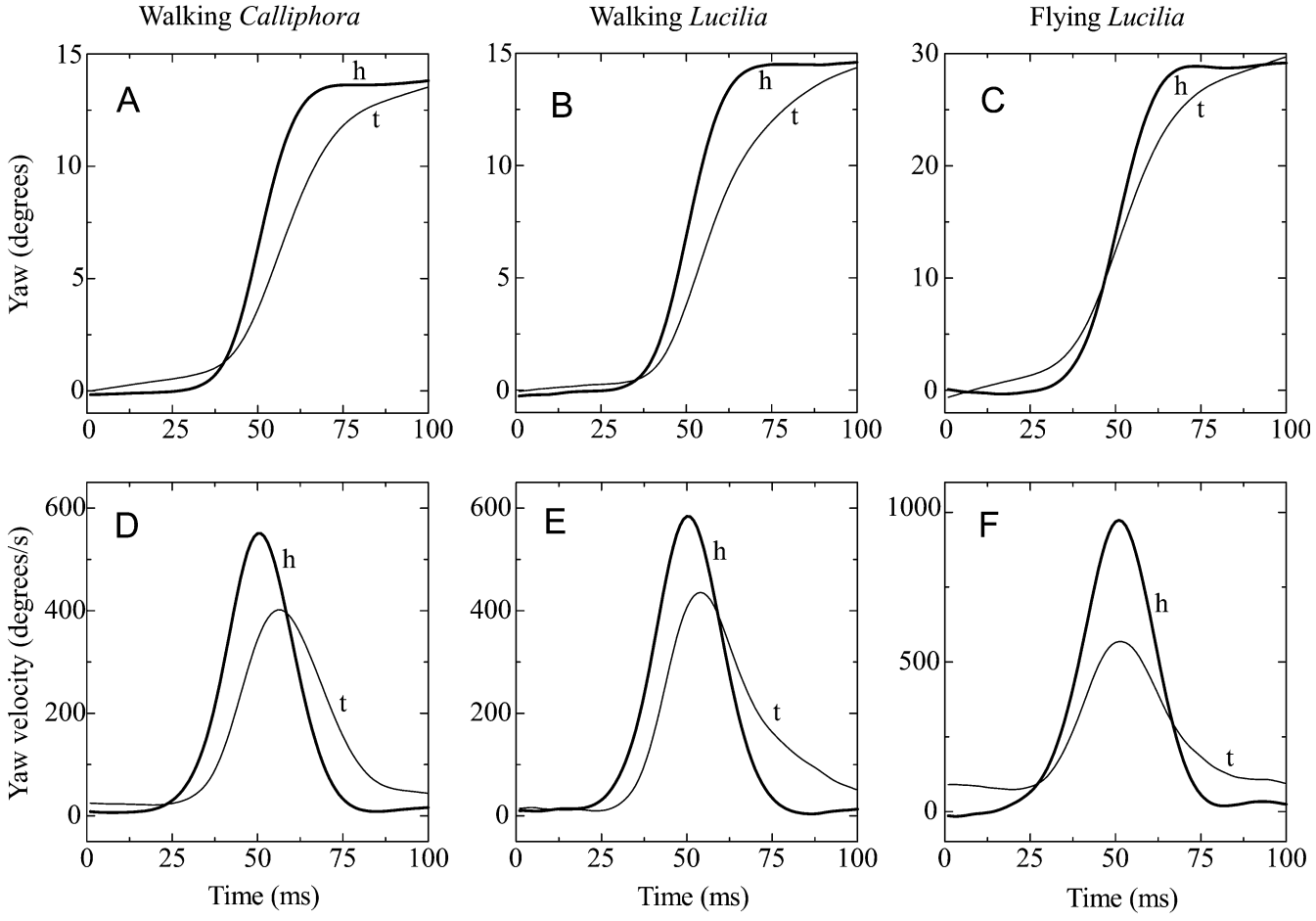

Fig. 4a–f Average yaw and yaw velocity during saccades, based on 1,550 saccades from walking *C. vicina*, 667 saccades from walking *L. cuprina* and *L. caesar*, and 176 saccades from flying *L. cuprina*. Averages are calculated for saccades of 10–20° in walking flies and 20–40° in flying flies. **a–c** Head (*h*) and thorax (*t*) yaw for walking *Calliphora* (**a**), walking *Lucilia* (**b**) and flying *Lucilia* (**c**). **d–f** Yaw velocity of head (*h*) and thorax (*t*) for walking *Calliphora* (**d**), walking *Lucilia* (**e**) and flying *Lucilia* (**f**). Note that yaw velocity peaks are aligned in flight, while in walking the peak velocity of the head occurs earlier than the peak velocity of the thorax

lines indicate head orientations and thin lines correspond to thorax orientation. Large changes in the orientation angles (yaw, pitch and roll) of the head and thorax are synchronized, with a frequency of approximately 10 Hz. These saccadic changes are abrupt, and between saccades the orientation is relatively steady. The difference between head and thorax orientation is usually small. While yaw, pitch and roll changes in flying flies occur in specific sequences—depending on the manoeuvre performed (Schilstra and van Hateren 1999), the pitch and roll of walking flies appear to be only weakly correlated with the yaw. Moreover, changes in pitch and roll are small compared with yaw changes, therefore we will concentrate on the investigation of yaw.

Thorax orientation during turns changes saccadically both in flying flies (Schilstra and van Hateren 1998b) and in walking flies (Fig. 2). The saccades of the thorax occur with a frequency of 5–10 Hz and between saccades the orientation is relatively stable. We found the saccades of the head and thorax from the peaks of their total angular velocities (in their own reference systems) and marked their positions in Fig. 1 with large dots (head) and small dots (thorax). It is apparent that, as in flying flies, each saccade of the thorax has a corresponding head saccade and they have roughly the same size. Unlike in flying flies, head saccades reach their peak velocity earlier than the corresponding thorax saccades.

The fine structure of the yaw during saccades can be obtained by averaging many saccades. From the total angular velocity of the head (in its own reference system) we detected the saccades of the head and averaged the yaws and yaw velocities in the 100-ms windows centred on the maxima of the angular velocity of the head. Averaged results from saccades to the right with sizes between 10–20° in walking flies and 20–40° in flying flies are shown in Fig. 4. The results are based on 1,550 saccades from walking *C. vicina*, 667 from walking *Lucilia* and 176 saccades from flying *Lucilia*. The results from walking *L. cuprina* and *L. caesar* are pooled because the average saccades from each individual fly measured from these two species were similar. Saccades to the left, and saccades of different sizes were similar (mirrored, respectively scaled). It is apparent that head

saccades have higher velocities and shorter durations than thorax saccades, both across species and for walking as well as flying.

In walking *Calliphora* and *Lucilia*, the head and thorax start rotating simultaneously, with the head turning faster than the thorax. The head reaches its maximum angular velocity approximately 5 ms earlier than the thorax, and has a higher peak angular velocity than the thorax. The head finishes its saccade earlier, and in the last part of the saccade the thorax still rotates while the head maintains its final orientation through a counter rotation with respect to the thorax. In flying *L. cuprina*, the average saccade is similar to the saccades described in flying *Calliphora* by van Hateren and Schilstra (1999): the times of the maximum angular velocities of the head and thorax coincide, and at the beginning and end of the saccades the thorax rotates while the head is kept stable, thus the head then rotates with respect to the thorax. The main difference between saccades during walking and flying is that head and thorax saccades are symmetrical during flight (their maximum angular velocities are aligned), while during walking they are asymmetrical (they are aligned by the starts of the saccades).

We divided walking episodes into two groups, one consisting of the periods around saccades, and the other consisting of periods between saccades. This separation can be obtained as follows: for each head saccade detected from the total angular velocity, we find the times when 10 and 90% of the head turn was completed, and we extend the resulting interval by 50% at the beginning and 100% at the end of saccades (different values are used because of the asymmetry of thorax and head yaw angular velocities). The episodes determined in this way will be defined as "during saccades", and the remaining walking will be defined as "between saccades". This algorithm yields a good approximation of the moments of onset and end of thorax orientation change. The proportion of time "between saccades" is slightly overestimated, because small saccades (below 2–3°) cannot be reliably discriminated from the noise. The proportion of the walking time that was classified as "during saccades" was 21%, with the remaining 79% classified as "between saccades". During saccades, the yaw velocities reach values of up to 1,500–2,000° s^{-1}, with the head and thorax 90% of the time slower than 580 and 500° s^{-1}, respectively. Between saccades, the yaw velocities are much lower than during saccades, with the head 90% of the time slower than 55° s^{-1} and the thorax 90% of the time slower than 110° s^{-1}.

Based on 5,713 saccades detected from three walking *C. vicina*, we calculated the average saccade duration versus saccade size and found that the duration of the saccades is approximately independent of the size of the saccades. This is related to the fact that yaw velocities of the head and thorax during saccades increase approximately linearly with the saccade size (Blaj 2004).

Discussion

The most important result of the experiments described in this article is that the head and thorax movements of both walking and flying blowflies are saccadic (operating with fast, abrupt turns). The saccades occur at a rate of 5–10 saccades s^{-1}. Regardless of the saccade size, head saccades last approximately 25 ms (10–90% of angular change), and thorax saccades last longer. Between saccades, the head and thorax are held almost stable, with the head more stable than the thorax. For the three species we investigated (*C. vicina*, *L. cuprina* and *L. caesar*), the saccades are similar, in accordance with the fact that these species are closely related. The saccades of walking and flying flies only differ in detail.

Head and thorax saccades occur almost simultaneously, probably as a consequence of the fact that the head can only rotate in the yaw direction (rotation about a vertical axis) by about 20° (Hengstenberg et al. 1986), thus large saccades require that the head and thorax saccades are synchronized. In flying *Lucilia*, the peaks of the yaw velocities of the head and thorax during a saccade occur at precisely the same time. The saccade of the head is faster, and the head is kept stable, by counter-rotations of the head, at the beginning and end of the thorax saccades. Van Hateren and Schilstra (1999) obtained similar results for flying *C. vicina*. In contrast, we found that in walking blowflies the peak of the thorax yaw velocity occurs approximately 5 ms later than the peak of the yaw velocity of the head. Furthermore, the thorax and head saccades are started simultaneously. Similar to flying flies, the head is held stable by a counter-rotation after the head completes its saccade and while the thorax still rotates. Walking saccades thus start simultaneously, while in flying saccades, peak angular velocities coincide. A possible reason for this difference between turns in walking and flying flies could be that in flying, turns are performed through a complex sequence of yaw, pitch and roll rotations (Schilstra and van Hateren 1999). An early head saccade might mechanically destabilise the fly through the counter-yaw induced in the thorax, or at least complicate the turning sequence. In walking flies, at least three legs (in tripod coordination) or four legs (tetrapod coordination) keep contact with the floor (Strauss and Heisenberg 1990), thus the legs can transfer the momentum induced by head rotations immediately to the floor. Blowflies might take advantage of this stability by rotating the head immediately.

Between saccades, the head has a higher probability than the thorax of low yaw, roll and pitch velocities. There are many systems contributing to this stabilisation of the head during walking: feedback using the rotational optic flow (Egelhaaf and Borst 1993; Krapp and Hengstenberg 1996), feedback from the halteres (Nalbach 1993), feedback from the prosternal organs (Preuss and Hengstenberg 1992), and feedback from leg proprioceptors (Hengstenberg 1992). The visual system is

tuned to slow rotations and the haltere system is tuned to fast rotations (*Drosophila*: Sherman and Dickinson 2003, 2004; Frye and Dickinson 2004). It is likely that between saccades the most important stabilisation system is the visual system. The halteres may mediate the stabilisation response of the head during the late phase of the thorax saccade in walking flies, and during both the early and late phases of the thorax saccade in flying flies. After the head saccade is completed and the thorax saccade is still finishing, the head remains stable by counter-rotating with respect to the thorax. A possible mechanism is that the walking saccade is initiated simultaneously in head and thorax and that the head stabilisation due to the haltere system is suppressed. When the head completes its saccade, the haltere stabilisation system becomes active and keeps the head stable while the thorax completes its saccade.

The duration of saccades in walking and flying blowflies is comparable: in flying flies, the duration varies slightly with saccade size, between 20 and 30 ms (Schilstra and van Hateren 1999), and in walking flies the duration of approximately 25 ms is independent of saccade size. The strong similarity between flying and walking saccades and saccade durations suggests that the same part of the blowfly brain controls the saccades in both flying and walking.

The 3D structure of the environment can be reconstructed from the translational optic flow (Koenderink 1986). Although the 3D structure can still be reconstructed from a complex optic flow containing both rotational and translational components (Longuet-Higgins and Pradzny 1980), the fact that blowflies increase the proportion of time with low angular velocities and thus low rotational optic flow makes it easier for the fly brain to process the optic flow. Rotations consume energy proportional to (a power of) the angular velocity due to the friction, and proportional to the squared angular velocity due to acceleration and deceleration. This energy is lost, thus saccadic changes of the orientation are less energy-efficient than corresponding non-saccadic changes would be. Apparently, this energy investment is justified by the resulting benefits for visual processing.

Blowflies walk in a saccadic-like manner, accelerating and slowing down with a frequency of 5–10 Hz (Fig. 2). The walking velocity and turning angular velocity are correlated: peaks in walking and turning velocity occur at approximately the same time, with the angular velocity peak occurring on average slightly before the walking velocity peak. Changes in the walking trajectory are largely independent of changes in orientation, but on average, the body axis tends to align with the walking trajectory. Flies often walk sideways, and angles of 45° between the orientation of the thorax and the tangent to the walking path are frequent. Between saccades, the head is typically aligned with the thorax, resulting in an eccentric translational optic flow. Due to the parallax, extraction of the 3D structure from the (translational) optic flow is more efficient for objects situated at right angles with the direction of translation, and flies might use sideways walking for improving the extraction of the 3D structure of the scene in front of the animal. In particular, flies might use the eccentricity of the optic flow for gauging the distance to objects. A similar function was suggested for lateral movements in the dolichopodid fly *Poecilobothrus nobilitatus* (Land 1993). The walking behaviour of blowflies is similar to the walking behaviour observed in *Drosophila* (Strauss and Heisenberg 1990; Wannek and Strauss 1996), which also shows large differences between the direction of walking and orientation, as well as similar turning patterns (Blaj 2004).

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